

Survey of parasitoids and hyperparasitoids (Hymenoptera) of the green peach aphid, *Myzus persicae* and the foxglove aphid, *Aulacorthum solani* (Hemiptera: Aphididae) in British Columbia

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ABSTRACT

We surveyed the parasitoids and hyperparasitoids of the green peach aphid, *Myzus persicae*, and the foxglove aphid, *Aulacorthum solani* in the lower Fraser Valley of British Columbia, Canada. Field surveys were conducted using isolated pepper plants, with aphids, as trap plants. Primary parasitoids recorded from field surveys were *Aphidius ervi*, *A. matricariae*, *Praon gallicum*, *P. unicum*, *P. humulaphidis*, *Ephedrus californicus*, *Diaeretiella rapae*, *Monoctonus paulensis*, *Aphelinus abdominalis* and *A. asychis*. *Diaeretiella rapae* only emerged from green peach aphids, and *Ephedrus californicus* only emerged from foxglove aphids. *Aphidius matricariae* was the most abundant primary parasitoid species reared from both aphid species. Hyperparasitoid species collected belonged to the genera *Dendrocerus*, *Asaphes*, *Alloxysta*, *Pachyneuron* and *Syrphophagous*. In greenhouses, *Dendrocerus carpenteri* was the dominant hyperparasitoid species. *Aphidius* and *Aphelinus* spp. were attacked by hyperparasitoids at similar rates. In the field, *Aphidius* spp. were attacked by five species of hyperparasitoid, and *Aphelinus* spp. were attacked by one, *Alloxysta ramulifera*. In general, the rate of attack by hyperparasitoids was much lower in field surveys than in our collections from greenhouses.

Key Words: *Aphidius*, *Aphelinus*, *Praon*, *Dendrocerus*, *Alloxysta*, *Asaphes*, greenhouse, biological control

INTRODUCTION

The green peach aphid, *Myzus persicae* (Sulzer) and the foxglove aphid, *Aulacorthum solani* (Kaltenbach) (Hemiptera: Aphididae) are serious pests of greenhouse pepper crops (Blümel 2004, Rabasse and van Steenis 1999). In greenhouses in British Columbia (BC), Canada, these aphids may be managed in part by introduction of four different parasitoid species: *Aphidius colemani* Viereck, *A. ervi* Haliday, *A. matricariae* Haliday, (Hymenoptera: Braconidae) and *Aphelinus abdominalis* (Dalman) (Hymenoptera: Aphelinidae). In BC and elsewhere, biological control of these pests periodically fails. A number of potential, and not mutually exclusive mechanisms may be responsible: e.g., differential susceptibility to parasitoids among aphid clones (Gillespie *et al.* 2009); mismatches between parasitoid virulence and aphid susceptibility (Henry *et al.* 2005); and mortality of primary parasitoids from hyperparasitoids (Brodeur and McNeil 1994).

We postulated that additional parasitoid species would be present in the environment outside of greenhouses, and that some of these might be useful additions to the biological control arsenal for these pest aphids. Survey approaches have identified locally-present natural enemies for the BC greenhouse industry in the past (Gillespie *et al.* 1997; McGregor *et al.* 1999). Moreover, considerable, potentially useful variation in key life history attributes have been shown to be present in populations of aphid parasitoids outside of greenhouses (Henry *et al.* 2010). Thus, it is reasonable to predict that additional parasitoid species would be present in the field and that at least some of these could be exploited as commercially-produced natural enemies. Moreover, field-derived variation in life-history attributes might be exploited to address the possible biotype mismatches cited above as causes of failures in aphid biological control.

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Growers and biological control advisors have long felt that hyperparasitoid attack on primary parasitoids of aphids is involved in the periodic collapse of biological control programs in greenhouses. Schooler *et al.* (2011) have recently shown, in greenhouse cage experiments, that a hyperparasitoid, *Asaphes suspensus* (Nees) (Hymenoptera: Pteromalidae: Asaphinae) is able to eliminate populations of an aphid parasitoid, *A. ervi*, attacking pea aphids *Acrythosiphum pisum* (Harris) (Hemiptera: Aphididae). However, little is known of the abundance or diversity of hyperparasitoids attacking the key primary parasitoids of aphid pests of greenhouse crops, either inside or outside of greenhouses. In order to study hyperparasitism-mediated

collapse of biological control, it is essential to know the identity of the species involved. Moreover, surveys might reveal species of primary parasitoids that are less susceptible to hyperparasitoid attack than the currently-available species.

We report here, the results of a survey of primary parasitoids and hyperparasitoids attacking *M. persicae* and *A. solani* on pepper, *Capsicum annuum* (L.) (Solanaceae). Our objectives were to inventory the diversity and relative abundance of parasitoids and hyperparasitoids of both *M. persicae* and *A. solani* in the lower Fraser Valley, British Columbia. We used pepper plants as trap plants in field exposures, to ensure relevance to the greenhouse system.

MATERIALS AND METHODS

Primary parasitoid survey

Surveys for primary parasitoids of *M. persicae* and *A. solani* were conducted at four locations in the lower Fraser Valley of British Columbia: Agassiz (N 49° 14.971' W 121° 45.498'), Abbotsford (N 49° 00.481' W 122° 20.024'), Langley (N 49° 06.583' W 122° 38.455'), and Ladner (N 49° 06.111' W 123° 10.251') from April to August 2005 and to a lesser extent in 2006.

As a survey tool, we used pepper plants, *Capsicum annuum* L., "Bell Boy" (Stokes Seeds, St. Catharines, Ontario, Canada), which hosted large populations of one of the two target aphid species. These were placed into survey sites for 3 days. Pepper plants were seeded in a soilless mixture (70% peat, 30% Perlite), transplanted to 1 L pots in soilless mixture after 2 weeks, and grown in a greenhouse under 16 h daylength. After 8 to 10 weeks, these were transplanted to a soilless medium (peat and perlite) in 4 L pots and used in surveys. We inoculated these plants with aphids from laboratory colonies. Excised pepper leaves containing approximately 200 mixed stages of either *M. persicae* or *A. solani* aphids were placed on pepper plants. The two target aphid species were each placed on different plants. Aphid populations increased in isolation cages on greenhouse benches for 7 to 14 days, prior to field exposure. At time of field exposure, each plant contained approximately 2000 aphids, and these were predominantly immature stages. Some alate

adults were present, but we did not determine the relative frequency of these.

Each pepper plant, with aphids was placed on a pedestal in a tray of water, and surrounded by a cylindrical cage, 43 cm dia x 56 cm tall, constructed of 1 cm square wire mesh. This cage prevented larger, generalist predators from accessing the aphids, and the tray of water mostly prevented slugs (Mollusca) from consuming the plant. Pepper plants at each location were placed in three separate sites within 500 m of each other within each location. Thus, there were six total plants (three with *M. persicae* and three with *A. solani*) at each of four locations on each survey date. After 3 days of exposure, the plants were collected, and held in 1m³cages covered with very fine mesh, on greenhouse benches. The plants were inspected daily and any mummies that formed were removed from the plant with a fine brush or on small leaf pieces that were cut from the plant with a scalpel. The mummies were placed individually in #00 gelatine capsules (T. U. B. Enterprises, Almonte, Ontario, Canada) for emergence of the adult parasitoid or hyperparasitoid. These were then either pointed on insect pins, or preserved in 70% ethanol, for taxonomic identification. A subset of material on insect pins was shipped to taxonomic specialists (primarily Dr. K. Pike, and Dr. M. Mackauer) for comparison with specimens in their collections. We used voucher material from these specialists, and

from the Canadian National Collection of Arthropods, Ottawa, combined with generic descriptions and taxonomic keys in van Achterberg (1997), and species descriptions and taxonomic keys in Ferrière (1965), Mackauer (1968), Graham (1976), Pike *et al.* (1977), Powell (1982), Johnson (1987), Mescheloff and Rosen (1990), Hayat (1998), Takada (2002) and Kavallieratos *et al.* (2005).

We investigated the effects of host species and location on diversity of parasitoids using a simple Berger-Parker dominance index (Southwood 1978). For each sample we calculated the abundance of the dominant species across all samples (*A. matricariae*) relative to the total number of individuals in the sample. An ANOVA model was used that included both of the above factors and their interaction, and because the dominance index is essentially a proportion, we transformed these data [$\arcsin(x^{0.5})$] for analysis, although we report the raw proportions. At each location, plants were located in three places separated by at least 500 m. Although these could be considered a form of pseudoreplication, we judged that the separation was sufficient to render these as independent samples, and we used this replication in the model. We also used date of placement as replication. Again, although this is not strictly correct, survey plants were not placed continuously at each location and we therefore considered each survey date as an independent sample of parasitoid diversity at the location.

Due to scheduling and handling time issues, plants were placed into sites at different times. Therefore, we could not use time of placement as an analysis variable. We grouped the results by month of exposure to hosts and host species, which allowed a visual analysis of the trends in parasitoid community composition for each host aphid.

Hyperparasitoid survey

We conducted both greenhouse and field surveys for hyperparasitoids. Surveys for hyperparasitoids of *M. persicae* and *A. solani* on peppers in greenhouses in British Columbia were done in four greenhouse operations, from June – October, 2006. These greenhouses had not been sprayed within 4

weeks of the survey date and had aphids and primary parasitoid mummies present. Mummies were collected from pepper plants and placed individually in #00 gelatine capsules as above. These were held until adult primary parasitoids or hyperparasitoids emerged. Adult hyperparasitoids were preserved in 70% ethanol and later identified to species. We stopped surveys when greenhouse operators treated with insecticides, mainly because live material was subsequently impossible to find.

Field surveys for hyperparasitoids of *M. persicae* and *A. solani* were conducted at four locations in the lower Fraser valley of British Columbia: Agassiz (N 49 14.971' W 121 45.498'), Abbotsford (N 49 00.481' W 122 20.024'), Langley (N 49 06.583' W 122 38.455'), and Ladner (N 49 06.111' W 123 10.251'), monthly from May to August 2005 and at least four plants with each aphid host were placed at each location on each date. Aphids were exposed at survey sites for three days, using the same methods as for the primary parasitoid survey. These plants were returned to the greenhouse at the research centre and held in cages until mummies began to form. When mummies began to form, the plants were then returned to the field locations for 3 days. At this time the survey plants contained both fully formed mummies and parasitoid larvae inside hosts. This provided opportunities for both endophagous (female wasp deposits eggs inside the primary parasitoid larva while it is still developing inside the live aphid, before aphid is mummified) and ectophagous (female wasp deposits her egg on the surface of the primary parasitoid larva or pupa after the aphid is killed and mummified) hyperparasitoid species to find hosts. When the plants were returned to the greenhouse the mummies, and any that formed afterward, were removed from plants as above and held for emergence of primary or hyperparasitoid species. We used taxonomic keys and species descriptions in Graham (1969), Andrews (1976), Fergusson (1980), Powell (1982), Pike *et al.* (1997), and Gibson and Vikberg (1998) to identify the specimens to the species level.

RESULTS AND DISCUSSION

Primary parasitoids

Nine primary parasitoid species were identified from each of the aphid species (Table 1). In addition, a small number of unidentifiable *Aphidius* and *Aphelinus* specimens were reared. The diversity and relative abundance of primary parasitoid species was almost identical between the two pest species (Table 1). *Diaretiella rapae* (M'Intosh) (Hymenoptera: Braconidae) was only reared from *M. persicae*, and *Ephedrus californicus* Baker (Hymenoptera: Braconidae) was only reared from *A. solani*. In general, fewer primary parasitoids were collected from pepper plants baited with *A. solani*, than from those baited with *M. persicae*. This is likely because *A. solani* drops from plants in response to parasitoid attack (Gillespie and Acheampong 2012), resulting in fewer parasitoid offspring on the plants. In comparison, we have observed that *M. persicae* rarely drops from plants in response to parasitoid attack.

Mackauer and Starý (1967) recorded 34 described species attacking *M. persicae* and 15 attacking *A. solani*. Records for *Aphelinus* spp. in Dunn (1949), Schlinger and Hall (1960), Shands *et al.* (1965), Mackauer (1968) and Kavallieratos *et al.* (2010) add an

additional four species for *M. persicae* and one for *A. solani*. Based on published surveys, the number of parasitoids actually reared from *M. persicae* in any given region ranges from five to ten, and for *A. solani*, from one to five. The dominant complex on both hosts generally consists of one or two *Aphidius* spp, a *Praon* species and an *Aphelinus* species. Our survey recorded no new parasitoid associations for *M. persicae*. The primary parasitoid community that we found attacking *M. persicae* is very similar to that found elsewhere. The primary parasitoid community attacking *A. solani* is considerably more diverse than found elsewhere. This may be due to our survey methods, which entailed placing hosts into the field on isolated plants, as opposed to the plant inspection and general collection methods used by others. It appears that *Praon gallicum* Starý, *P. humulaphidis* Ashmead, *Monoctonus paulensis* (Ashmead) and *Ephedrus californicus* Baker (Hymenoptera: Braconidae) have not been reared previously from *A. solani*, and thus these constitute new host records.

The generalist parasitoid, *Aphidius matricariae* Haliday (Hymenoptera: Braconidae), was the most abundant species on both aphid species (Table 1). It has been

Table 1

Percent of species in the parasitoid complex of *Myzus persicae* and *Aulacorthum solani*, reared from pepper plants with the indicated aphid species exposed in the field at four different locations in 2005 and 2006.

Primary parasitoid	Aphid host	
	<i>Myzus persicae</i>	<i>Aulacorthum solani</i>
<i>Aphidius ervi</i>	6.7	3.9
<i>Aphidius matricariae</i>	48	54.7
<i>Aphidius</i> spp.	0.7	1.7
<i>Praon gallicum</i>	3.5	10.1
<i>Praon unicum</i>	15.5	4.1
<i>Praon humulaphidis</i>	0.2	1
<i>Diaretiella rapae</i>	1.2	0
<i>Aphelinus asychis</i>	3.6	0.2
<i>Aphelinus abdominalis</i>	16.7	21.1
<i>Aphelinus</i> spp.	1.2	0.5
<i>Monoctonus paulensis</i>	0.5	0.3
<i>Ephedrus californicus</i>	0	0.3
Hyperparasitoids	1.7	0.3
Total number reared	2585	583

recorded as the dominant parasitoid of *M. persicae* by many authors (e.g., Dunn 1949, Schlinger and Hall 1960, Mackauer 1968, Shands *et al.* 1972, Devi *et al.* 1999). It is known to be effective for the control of the green peach aphid on sweet pepper (Rabasse and Shalaby 1980). This species was apparently accidentally introduced into North America (Schlinger and Mackauer 1963, Mackauer 1968). However, it was reported to be reared at the Belleville biological control laboratory [under a synonym, and as a native, *Aphidius phorodontis* Ashmead (Hymenoptera: Braconidae)], and widely shipped to Canadian greenhouse growers for biological control of *M. persicae* in 1938, 1939 and 1940 (McLeod 1962). It is presently commercially reared for release as a biological control agent, particularly for control of green peach aphids. *Aphidius matricariae* has not previously been reported to be abundant on *A. solani* although it has been reared from this host (Mackauer and Starý 1967, Dunn 1949, Kavallieratos *et al.* 2010). Laboratory experiments indicate that under choice conditions, *A. matricariae* selects *M. persicae* as hosts in preference to *A. solani* (Acheampong & Gillespie unpublished data). The abundance of *A. matricariae* on *A. solani* may simply be due to an abundance of *A. matricariae* adults in the habitat, either because of the concentrations of hosts and honeydew signals on our trap plants (Bouchard and Cloutier 1985) or the abundance of alternative hosts in the habitats in which we placed our survey plants. Because we did not survey abundance of parasitoid adults in those habitats, there is no evidence to support either of these competing explanations.

Aphidius ervi Haliday, which is currently released in greenhouses for biological control of *A. solani* and *Macrosiphum euphorbiae* (Thomas) (Hemiptera: Aphididae) by some growers in BC, was less common than *A. matricariae*. This species was introduced into western North America from Europe in the 1960s for biological control of pea aphids, *Acyrtosiphon pisum* (Harris) (Hemiptera: Aphididae) (Mackauer and Starý 1967). Although there are field collection records of *A. ervi* from both *M. persicae* and *A. solani* (e.g. Kavallieratos *et al.* 2010) this parasitoid is not widely reared in the field from either

host. Takada and Tada (2000) did not rear this species from field collections of either host in Japan, and Mackauer and Starý (1967) considered records on *A. solani* and *M. persicae* to be suspect. Henry *et al.* (2005, 2006) found that *A. ervi* is not particularly adapted to using *A. solani* as hosts until it has been reared for several generations on that host.

It is important to note that we did not rear any specimens of *Aphidius colemani* Viereck (Hymenoptera: Braconidae). This species is intensively released for biological control of aphids in greenhouse crops in the region. It has been recovered from cereal fields in Germany, where it is also released for biological control of aphids in greenhouses (Adisu *et al.* 2002). It is conceivable that some specimens of this species were present among the *A. matricariae* specimens. The species are very similar in general appearance (M. Mackauer, pers. comm.), and some could have been overlooked. Pike *et al.* (1996) report a single specimen of *A. colemani* reared from an unidentified aphid in Washington State. A molecular analysis of field collections of *A. matricariae* is likely needed to resolve this question in British Columbia.

Aphelinus asychis Walker and *Aphelinus abdominalis* (Dalman) (Hymenoptera: Aphelinidae) were present on both *M. persicae* and *A. solani*. *Aphelinus abdominalis* was more abundant than *A. asychis* on both hosts. *Aphelinus abdominalis* is of European origin, and has been used extensively for biological control of aphids in greenhouses in North America since 1998 (Gillespie *et al.* 2002), but it is not clear if this application was the first release in North America. It is extensively released for biological control of aphids in greenhouses in British Columbia. *Aphelinus asychis* was released into North America in Texas, for biological control of *Schizaphis graminum* (Rondani) (Hemiptera: Aphididae) in the late 1960s (Jackson 1971) and has since been widely re-distributed. Neither species is recorded in any of the earlier general field surveys in North America (MacGillivray and Spicer 1953; Shands *et al.* 1955, 1965; Schlinger and Hall 1960). Mackauer (1968) reports *A. asychis* to be a parasitoid of *M. persicae* in Europe and *A. semiflavus* Howard to fill the same role in North America. *Aphelinus semiflavus* is

widely recorded as a parasitoid of *M. persicae* and *A. solani* but this species was not reared in our survey. In Japan, *A. solani* was not a suitable host for *A. abdominalis*, but was highly suitable for *A. asychis* (Takada 2002). Our survey results suggest an opposite trend, but the abundance of *A. abdominalis* could be an artifact resulting from a combination of releases in protected agriculture combined with an abundance of highly suitable alternative hosts in the field.

Of the remaining parasitoid species, the *Praon* spp. were common as a group. *Praon unicum* Smith was common on *M. persicae*, and *P. gallicum* on *A. solani*. *Praon humulaphidis* Ashmead was not reared during extensive surveys in 2005, but was reared from both hosts during selected exposures of aphids on pepper plants in 2006, and so is included as a host record in the survey results. Johnson (1987) reports that *P. gallicum* was introduced into North America for biological control of *S. graminum*, and that a *Praon* sp. reported by Shands *et al.* (1965) on both *A. solani* and *M. persicae* was actually *P. gallicum*. Thus this species is either native to North America, or was introduced at some time previous to 1965, and it is important to note that the species was not described, from European specimens, until 1971 (Starý 1971). Jansen (2005) reared *P. gallicum* from both *A. solani* and *M. persicae* in a survey in Belgium, and Schlinger and Hall (1960) reared *P. unicum* from *M. persicae* in Riverside, CA. Raworth *et al.* (2008) reported *P. unicum* to be important in the regulation of aphid populations on blueberry (*Vaccinium corymbosum*). Other surveys have found different *Praon* spp. on the two aphid hosts, particularly *Praon volucre* Haliday in Europe, and *Praon occidentale* Baker in North American surveys. In general, species in this genus are consistently present in surveys, but are not particularly abundant. Species of both *Aphidius* and *Aphelinus* are exploited as commercially reared biological control agents, but at this time, no *Praon* spp. are reared for release against *M. persicae* or *A. solani* in North America.

The diversity of parasitoids, based on the Berger-Parker dominance index (Number of *A. matricariae*/total parasitoids from the location) was different between locations (0.67 ± 0.093 , 0.20 ± 0.103 , 0.58 ± 0.133 and

0.41 ± 0.115 for Abbotsford, Agassiz, Ladner and Langley, respectively; Anova, F3, 55 = 3.26, P = 0.0279). The Agassiz samples were the most diverse (least dominated by *A. matricariae*), compared to the Abbotsford (most dominated by *A. matricariae*), and the samples from Langley and Ladner were intermediate, and not different from each other or the extremes. The Berger-Parker dominance index was also affected by aphid species (F1, 55 = 10.40, P = 0.0021), with the samples from *M. persicae* being considerably more dominated by *A. matricariae* than those from *A. solani* (0.62 ± 0.075 and 0.28 ± 0.082 , for *M. persicae* and *A. solani*, respectively). The differences between the two aphid species are not surprising since *A. matricariae* is a dominant parasitoid on *M. persicae* in almost all literature reports, whereas this parasitoid is not often recorded from *A. solani*. The differences between locations may reflect a number of factors relating to both plant community and agronomic practice in the different locations. For example, plants at the Agassiz location, were located in proximity to native forest habitat with considerable plant diversity, and were not bordered on all sides by agricultural habitat. In contrast, the Abbotsford plants were in close proximity to commercial raspberry production, with comparatively low plant diversity. The differences in plant diversity may imply similar differences in aphid and parasitoid diversity in surrounding habitats, but these ideas are preliminary, and would need to be tested rigorously with better-designed surveys.

The proportion of each parasitoid species on the two aphid hosts appeared to vary through the survey period. *Aphidius matricariae* was almost absent on *M. persicae* in April, although it was the dominant parasitoid thereafter. Conversely, *A. matricariae* was relatively common on *A. solani* in April and May, and generally decreased in abundance thereafter. *Praon unicum* was only present on both species in the May samples, which is consistent with the observations of Raworth *et al.* (2008), who found that this parasitoid is an early-season species on *Vaccinium*. *Aphelinus abdominalis* was abundant on *M. persicae* in April, yet did not continue to be common, whereas on *A. solani* this parasitoid was common throughout the survey. There are a number of other trends

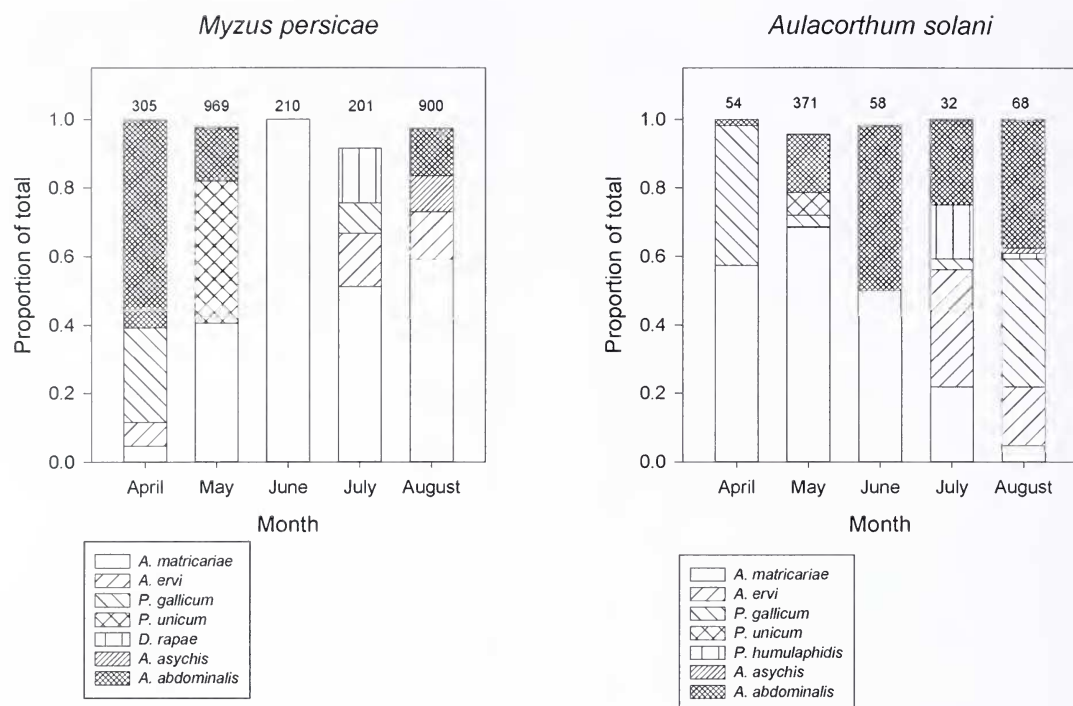


Figure 1. Proportion of parasitoids reared from *M. persicae* and *A. solani* during five months of sampling at four locations in British Columbia. The numbers over each bar represent the total number of primary parasitoids on which the proportions are based.

in species composition that could be constructed from Figure 1. However, these data are derived primarily from one year of survey so it is not clear if the trends apply to all years or are unique to the survey period. Again additional survey is required to determine if these are valid trends.

Hyperparasitoids

The primary parasitoid survey yielded a relatively low frequency of hyperparasitoids (Table 1). This was likely due to the relatively short exposure time, which removed hosts from the field before mummies had formed. In hyperparasitoid surveys, we placed plants back into the field after mummies of the primary parasitoids had begun to form, and we found considerably greater diversity and abundance of hyperparasitoids.

From primary parasitoid mummies that we placed into our field survey locations we reared six species of hyperparasitoids, and two other species we could only identify to genus (Table 2). Collectively, the *Alloxysta* spp. (Hymenoptera: Charipidae: Alloxystinae) were the majority of the hyperparasitoids. *Dendrocerus carpenteri* (Curtis)

(Hymenoptera: Megaspilidae) was next in abundance, and was the single most abundant species. Three *Asaphes* species (Hymenoptera: Pteromalidae) comprised the remainder. Although the majority of the hyperparasitoid species were reared from *Aphidius* species, *Aphelinus* species were attacked by *Alloxysta ramulifera* Thompson, and *Praon* mummies were attacked by an *Alloxysta* sp., and by *Asaphes suspensus* (Nees). The aggregate rate of hyperparasitism did not exceed 10% in any collections (Table 2). It is important to note that this intensity of attack resulted from exposure of mummies and maturing larvae of the primary parasitoids for only three days, and that these plants had also been previously exposed in the field to collect a community of the primary parasitoids. Longer exposures would likely have resulted in higher rates of hyperparasitism. We do not record the primary parasitoid host to species because we could not be absolutely sure of the identity of the mummies. However, based on the primary parasitoid survey, the majority of hosts were *A. matricariae*, and *Aphelinus abdominalis*. All of the associations between primary

Table 2

Numbers of hyperparasitoid species emerging from primary parasitoid mummies exposed in the field at four different locations in British Columbia, 2005

Location	Month	# of plants	# of plants with primary parasitoids	# of plants with hyperparasitoids	# of primary parasitoids	# of hyperparasitoids	Hyperparasitoid species	Host mummy
Abbotsford	April/May	12	9	0	198	0		
	June	16	13	1	637	4	<i>Alloxysta</i> sp.	<i>Aphidius</i>
	July	12	11	1	340	10	<i>Dendrocerus carpenteri</i>	<i>Aphidius</i>
	August	23	15	5	429	19	<i>Dendrocerus carpenteri</i>	<i>Aphidius</i>
							<i>Alloxysta</i> sp.	<i>Aphidius</i>
							<i>Asaphes suspensus</i>	<i>Aphidius</i>
							<i>Asaphes</i> sp.	<i>Aphidius</i>
	September	8	3	0	70	0		
	Agassiz	April/May	12	4	0	39	0	
June		16	12	2	737	1	<i>Alloxysta</i> sp.	<i>Praon</i>
						2	<i>Alloxysta</i> sp.	<i>Aphidius</i>
July		12	7	1	359	2	<i>Alloxysta victrix</i>	<i>Aphidius</i>
August		20	10	0	742	0		
September	12	6	1	99	4	<i>Asaphes suspensus</i>	<i>Praon</i>	
Ladner	April/May	12	7	0	344	0		
	June	16	11	3	740	26	<i>Asaphes californicus</i>	<i>Aphidius</i>
	July	12	11	5	495	3	<i>Alloxysta victrix</i>	<i>Aphidius</i>
						47	<i>Alloxysta brassicae</i>	<i>Aphidius</i>
August	20	10	0	530	0			
Langley	April/May	12	5	1	288	17	<i>Dendrocerus carpenteri</i>	<i>Aphidius</i>
	June	16	12	1	140	1	<i>Dendrocerus carpenteri</i>	<i>Aphidius</i>
	July	12	11	4	437	16	<i>Alloxysta brassicae</i>	<i>Aphidius</i>
						1	<i>Alloxysta</i> sp.	<i>Aphelinus</i>
						10	<i>Alloxysta victrix</i>	<i>Aphidius</i>
	August	20	13	2	1070	30	<i>Alloxysta ramulifera</i>	<i>Aphelinus</i>
73						<i>Alloxysta ramulifera</i>	<i>Aphelinus</i>	

parasitoid genera and hyperparasitoids have been previously recorded.

We identified six hyperparasitoid species attacking primary parasitoid mummies collected from greenhouses, and reared a further three species that we could identify only to genus (Table 3). In all the greenhouses surveyed, *D. carpenteri* was the most abundant hyperparasitoid species (Table 3). The hyperparasitoid complexes were quite different between the two most common primary parasitoid mummy types. The majority of hyperparasitoids that emerged from *Aphidius* mummies in all greenhouses were *D. carpenteri*. This species was also

present on *Aphelinus* mummies, but was not the dominant hyperparasitoid on that host in any greenhouse. Three *Asaphes* species collectively dominated the community of hyperparasitoids attacking *Aphelinus* mummies. Only one *Praon* mummy was collected from the greenhouse survey and an *A. suspensus* hyperparasitoid emerged from it. The community of hyperparasitoids appears to be quite different between field and greenhouse collections. In the field, the *Alloxysta* species dominated and *Asaphes* spp. were not common. In contrast, the *Asaphes* species were common in greenhouses while the *Alloxysta* spp. were not. *Asaphes* spp. have

Table 3

Numbers of hyperparasitoids emerging from primary parasitoid mummies collected from pepper plants in greenhouses in British Columbia, 2006

Greenhouse	Primary parasitoid genus	# of primary parasitoids	# of hyper-parasitoids	<i>D. carpenteri</i>	<i>A. californicus</i>	<i>A. suspensus</i>	<i>Asaphes</i> sp	<i>Pachyneuron aphidis</i>	<i>A. brassicae</i>	<i>A. vicatrix</i>	<i>Alloxysta</i> sp.	<i>Syrphophagus</i> sp.
A	Aphidius	324	28	25	3	0	0	0	0	0	0	0
A	Aphelinus	0	0	0	0	0	0	0	0	0	0	0
B	Aphidius	114	75	40	0	0	0	35	0	0	0	0
B	Aphelinus	12	6	0	0	3	0	3	0	0	0	0
C	Aphidius	1340	129	84	9	19	0	10	1	4	0	2
C	Aphelinus	64	3	1	0	0	0	0	0	0	2	0
C	Praon	1	1	0	0	1	0	0	0	0	0	0
D	Aphidius	254	217	152	20	32	7	3	1	0	2	0
D	Aphelinus	85	43	20	9	9	5	0	0	0	0	0
Total ¹			502	322	41	64	12	51	2	4	4	2
Percent ²				64.1	8.2	12.7	2.4	10.2	0.4	0.8	0.8	0.4

1. Total primary parasitoid mummies collected from greenhouses

2. Percent of each species in the total hyperparasitoid community

a higher temperature threshold than their parasitoid hosts (Campbell *et al.* 1974) and might therefore be more successful in greenhouse than in field settings. *Dendrocerus carpenteri* was common in both habitats. Although differences in the greenhouse and field environments might account for the differences in hyperparasitoid communities, it is equally possible that community assembly has a strong random component, and that the community that we found in our surveys is determined to a large extent in both habitats by which species are the first invaders.

The greenhouses each had quite different histories, and thus we did not pool data for these surveys (Table 3). Greenhouse A, where the hyperparasitism rate was low, was treated with insecticides for a pest other than aphids, and sampling was discontinued. In greenhouse B, the hyperparasitism rate – i.e., the percent of primary parasitoid mummies that yielded a hyperparasitoid – was high (60.32%) in July, and the greenhouse was treated for aphids with an insecticide. Hyperparasitism peaked in greenhouse C in August (61.54%) and in greenhouse D at the end of August and early September, at 77.78 and 77.38% respectively. Greenhouse D was sprayed for aphids in September and the survey was terminated. Greenhouse C, a propagation house at the Agriculture and Agri-Food Research Centre, Agassiz, was not sprayed during the survey

period. For greenhouse C, there was an increase in hyperparasitism from June to July and a peak level of hyperparasitism, with a subsequent decrease in hyperparasitism rate in September and October. Across all greenhouses, the level of hyperparasitism of primary parasitoid species was similar for *Aphidius* and *Aphelinus* species, at 32.28 and 34.78%, respectively. This demonstrates that the two genera are equally vulnerable to attack by hyperparasitoids in greenhouses. *Alloxysta ramulifera* was the dominant hyperparasitoid species reared from *Aphelinus* species in the field. This species was not collected from the greenhouse survey. The recovery of hyperparasitoid species from *Aphelinus* is particularly significant, as this species is thought to not be attacked by hyperparasitoids in greenhouse systems. There may be undiscovered impacts of hyperparasitoids on *Aphelinus* in greenhouses in BC which could worsen if *A. ramulifera* migrates from the field into greenhouses.

Hyperparasitism could be a limiting factor in the biological control of aphids in greenhouses, since these are essentially large cages with limited opportunities for refuge for the primary parasitoid hosts. Mackauer and Völkl (1993) argued that hyperparasitoids would be unable to limit the actions of primary parasitoids of aphids because of low lifetime fecundity and limited egg supply in the hyperparasitoids, as long as the parasitoids

are able to escape by dispersal. Schooler *et al.* (2011) demonstrated that *Asaphes suspensus* could drive *Aphidius ervi* to extinction after four generations in large multiple-plant cages, and their result is highly relevant to greenhouse agriculture. In our greenhouse surveys, a high rate of hyperparasitism was associated with the collapse of biological control of aphids, but it was not clear that there was a causal relationship.

The objectives of our survey were to identify parasitoid species in the community in BC that could potentially be exploited as

biological control agents for *M. persicae* and *A. solani* in greenhouse crops. We identified three *Praon* species that could be further evaluated. *Aphelinus asychis* and *Aphidius matricariae* occurred on *A. solani* and might be host-adapted strains that could be integrated into biological control programs. We surveyed the biodiversity of hyperparasitoids and demonstrated that there are several species that might be of concern, but their impacts on population dynamics require further study.

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